

Paragoniastrea variabilis Kishi, Nomura & Fukami, sp. nov. (Cnidaria, Anthozoa, Scleractinia), a new coral species previously considered as a variant of *Paragoniastrea deformis*, from Japan and northern Taiwan

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Abstract

A new zooxanthellate scleractinian coral, *Paragoniastrea variabilis* Kishi, Nomura & Fukami, **sp. nov.** (Scleractinia, Merulinidae), is described from non-coral reef regions of Japan and northern Taiwan. This new species was previously recognized as a morphological variant of *Paragoniastrea deformis* (Veron, 1990) and can be morphologically distinguished from that species by lacking groove-and-tube structures on corallite wall joints, and by having larger calices, numerous septa, and up to three corallites in one valley. The new species also formed an independent clade from its congeners, *P. australensis* (Milne Edwards & Haime, 1857), *P. deformis* and *P. russelli* (Wells, 1954), in the molecular phylogeny based on the mitochondrial intergenic region and nuclear ribosomal internal transcribed spacers.

Key words: Merulinidae, molecular phylogeny, taxonomy, temperate region, zooxanthellate scleractinian corals

Introduction

The zooxanthellate scleractinian coral genus *Paragoniastrea* Huang, Benzoni & Budd, 2014, which belongs to the family Merulinidae Verrill, 1865, inhabits the Indo-Pacific region (Huang et al. 2014). Currently, this genus contains three species, namely, *P. australensis* (Milne Edwards & Haime, 1857), *P. deformis* (Veron, 1990), and *P. russelli* (Wells, 1954), which were transferred from other merulinid genera, *Favites* or *Goniastrea*, to this genus based on molecular phylogenetic and morphological data (Huang et al. 2014). *Paragoniastrea* is characterized by encrusting or massive colony morphology, plocoid, cerioid or meandroid in corallite arrangements, and developed paliform lobes. These

characteristics are similar to those of *Favites* and *Goniastrea*, but *Paragoniastrea* is distinguished from these genera by its distinct phylogenetic affinities (Huang et al. 2014; Quek et al. 2023) and several morphological differences in corallite characteristics, such as the height of calice relief, septa (number, tooth height, and spacing), and theca structure (Huang et al. 2014).

Paragoniastrea deformis, described from Kushimoto, Wakayama, mainland Japan, is mainly distributed around the warm-temperate, non-coral reef region of Japan (Veron 1990, Nishihira and Veron 1995). Although *P. deformis* has also been reported from the Philippines (Wilfredo and Emmi 2003), whether it is the same species or not remains unknown because the specimen (P1L01316) shown by Wilfredo and Emmi (2003) has corallites approximately twice as large as the holotype and has up to three distinct corallites in a valley between corallite walls. *Paragoniastrea deformis* is known to have groove-and-tube structures (groove-and-tubercle structure *sensu* Rosen 1968) on corallite wall joints. Groove-and-tube structure is defined as a feature of vertical and horizontal intercommunicating holes between adjacent corallites, some of which are formed around corallites by parasitic worms (Rosen 1968; Randall and Eldredge 1976). This character has been used as a specific morphological characteristic in some species, including *P. deformis* and *Favites valenciennesii* (Milne Edwards & Haime, 1849) (Veron 1990). However, some colonies of *P. deformis* do not have any groove-and-tube structures, and they are considered to be intraspecific morphological variations of *P. deformis* (Nishihira 1991; Uchida and Soyama 1994; Nishihira and Veron 1995; Veron 2000; Veron et al. 2016). Huang et al. (2014) reported that two specimens of *P. deformis* (*Paragoniastrea* sp.) with a non-groove-and-tube type were separated from typical *P. deformis* with groove-and-tube structures by molecular phylogenetic analysis. To date, morphological and molecular phylogenetic analyses for the non-groove-and-tube type of *P. deformis* remain insufficient to define it as a species different from typical *P. deformis*. Groove-and-tube structure is recognized as one of the key species-specific morphological characters in *Favites valenciennesii*. Thus, this structure might be a good key character to define species in this genus.

This study has shown that the non-groove-and-tube type of *P. deformis* is distinct from *P. deformis* in both morphology and phylogeny, and describes a new species, *Paragoniastrea variabilis* sp. nov. In addition, three specimens without groove-and-tube structures but distinguished from *P. variabilis* sp. nov. by their distinct phylogenetic affinities and slight morphological differences were tentatively designated as *P. aff. deformis* as it is not yet clear if they represent a different species or not from *P. deformis*.

Materials and methods

Materials

Sampling of materials was conducted at seven sites (Shirahama and Kushimoto, Wakayama; Fukashima Island, Oita; Takashima Island, Nagasaki; Shimamourashima Island and Oshima Island, Miyazaki; Amakusa, Kumamoto) in Japan and at one location (Yehliu, New Taipei) in northern Taiwan (Fig. 1, Suppl. material 1). For comparison with the new species, we examined the holotype of *P. deformis* (MTQ G61876) and the photographic images of holotypes of

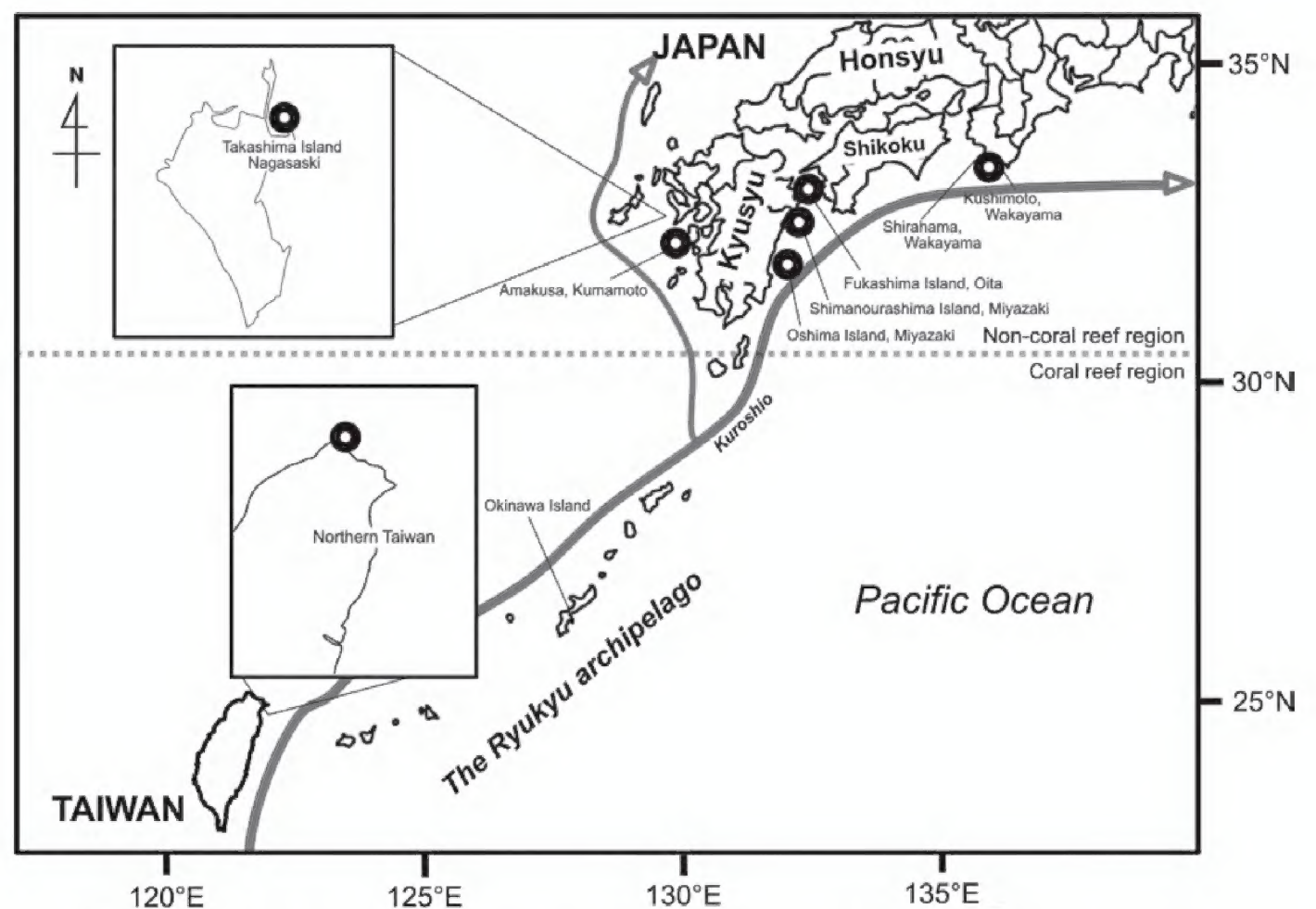


Figure 1. Sampling sites (black circles) where we collected skeletal and genetic samples in this study.

P. australensis (MNHN IK-2010-409) and *P. russelli* (USNM 45004). Specimens of other *Paragoniastrea* species collected at the same sites were also used (Suppl. material 1). Samples were collected by a hammer and chisel to break only the necessary size (around 10 cm³) for morphological analysis.

A small piece (<1 cm³) was also cut from each collected sample with nippers for molecular phylogenetic analysis and was mixed with a guanidine solution (4M guanidine thiocyanate, 0.1% sodium N-laurylsarcosine, 10 mM Tris-HCl pH 8.0, 0.1M 2-mercaptoethanol; Fukami et al. 2004) to dissolve tissues. The remaining samples were bleached and labeled with numbers associated with the collection sites, and they were stored as skeletal specimens for use in morphological analysis.

The holotype and two paratypes of *Paragoniastrea variabilis* sp. nov. have been deposited in the Department of Marine Biology and Environmental Sciences, University of Miyazaki (MUFS) in Miyazaki, Japan. The other specimens were deposited in the following institutions: Seto Marine Biological Laboratory (SMBL), Wakayama, Japan; Sabiura Marine Park Research Station (SMP), Wakayama, Japan, and Zoological Collection, Biodiversity Research Museum, Academia Sinica (ASIZC), Taipei, Taiwan. Museum abbreviations for type materials are as follows: Muséum national d'Histoire naturelle de Paris (MNHN, France), Museum of Tropical Queensland (MTQ, Australia), and National Museum of Natural History, Smithsonian Institution (USNM, USA).

Morphological analysis

Measurements and observations of the skeletal specimens from Japan were made using a digital microscope (Keyence VHS-1000; WRAYMER WRAYC-AM-NOA630 + Leica MZ16) and a scanning electron microscope (Hitachi High-Tech TM-1000). Taiwan specimens were photographed by a digital camera

(OM system Tough TG-6) and the skeletal image was measured by Image J (version 1.5.3, <https://imagej.net/ij/index.html>).

To analyze the morphological differences between *P. variabilis* sp. nov. and *P. deformis*, morphological characteristics were compared using the Brunner-Munzel test or the Welch t-test, after confirming normality and homogeneity. In addition, principal component analysis (PCA) was performed on morphological data of *P. variabilis* sp. nov., *P. deformis* and *P. aff. deformis*, which were measured and standardized in this study. PCA was performed using the `prcomp` function in R version 4.3.1 (The R Foundation for Statistical Computing <http://www.R-project.org>). The PCA result was plotted using the R packages *devtools* and *ggbiplot*. The specimens shown in Suppl. material 1 were used in these analyses.

Molecular phylogenetic analysis

Total genomic DNA was extracted from each guanidine sample by the conventional phenol-chloroform extraction method. Using the extracted DNA, mitochondrial intergenic region (IGR) and nuclear ribosomal internal transcribed spacers (ITS) were amplified by the PCR method. Primers used for each marker were MCOIF3 (5'- CCA AGA CGA TAT TTC GGA CTT -3') and tRNAm^{et}R (5'- GTG AGA CTC GAA CTC ACT TTT TT -3') for IGR (Mitsuki et al. 2021), 1S (5'- GGG TAC CCT TTG TAC ACA CAC CGC CCG TCG CT -3') and 2SS (5'- GCT TTG G GC GGC AGT CCC AAG CAA CCC GAC TC -3') for ITS (Wei et al. 2006). PCR was performed in each sample using 11.32 µL of sterile distilled water, 2 µL of 10×buffer, 2 µL of forward primer, 2 µL of reverse primer, 1.6 µL of dNTPs, 0.08 µL of exTaq and 1 µL of DNA of each sample. PCR conditions for ITS and IGR markers were 94 °C for 60 s followed by 35 cycles at 94 °C for 30 s, 55 °C for 45 s, and 72 °C for 90 s, and 72 °C for 5 mins for the final extension. However, for some samples with unsuccessful amplification, we used the following PCR conditions: 94 °C for 60 s, 94 °C for 30 s, 48 °C for 45 s, and 72 °C for 90 s, repeated 5 times, followed by 94 °C for 30 s, 55 °C for 45 s, and 72 °C for 90 s, repeated 30 times, and 72 °C for 5 mins for the final extension. The amplified PCR products were treated with shrimp alkaline phosphatase and exonuclease I at 37 °C for 40 mins and 80 °C for 20 mins.

DNA sequences were determined by direct sequencing using ABI3730 sequencers by a contracted research service (FASMAC Co. Ltd., Kanagawa, Japan). Alignments of IGR and ITS sequences were carried out using the E-INS-i option in MAFFT 7 online (<https://mafft.cbrc.jp/alignment/server/>) (Kuraku et al. 2013; Katoh et al. 2019) under default parameters. Molecular phylogenetic trees were reconstructed using the neighbor-joining (NJ) and maximum-likelihood (ML) methods after all indels were deleted in MEGA ver. 11.0 (Tamura et al. 2021). MEGA was also used to estimate a model of nucleotide evolution for each marker (HKY+G for IGR, T92+G for ITS markers) and to conduct a bootstrap analysis (with 1000 replicates). All DNA sequences obtained in this study were submitted to the DNA Data Bank of Japan (DDBJ) (accession numbers [LC804981–LC804999](#) for IGR, [LC801365–LC801368](#), [LC801370–LC801379](#) for ITS; Suppl. material 1).

The published DNA sequences of *Paragoniastrea* species used by Huang et al. (2014) for IGR and ITS were used to compare with our data (Suppl. material

2). There were many multi-peaks in the DNA sequences of ITS for two samples (sample numbers: JP009, JP065) used by Huang et al. (2014). Therefore, we newly extracted genomic DNA from one guanidine sample (JP065), which is stored at the University of Miyazaki and used in the analysis for ITS. For both the IGR and ITS trees, DNA sequences (accession numbers [KJ666508](#) and [KJ666509](#) for IGR, [KJ666394](#) and [KJ666396](#) for ITS) of *Merulina ampliata* from Huang et al. (2014) were used as outgroups.

Taxonomy account

Family Merulinidae Milne Edwards & Haime, 1857

Genus *Paragoniastrea* Huang, Benzoni & Budd, 2014

***Paragoniastrea variabilis* Kishi, Nomura & Fukami, sp. nov.**

<https://zoobank.org/CD11CAA7-81EA-4241-8DAE-BB1F80F5E406>

Figs 2–5

Japanese name: henge-kamenoko-kikumeishi

Goniastrea deformis: Nishihira 1991: 254, 1 unnumbered fig.; Uchida and Soyama 1994: 65, figs 13, 14; Nishihira and Veron 1995: 345 (part), 3 unnumbered color figs; Veron 2000: 167 (part), 6; Nomura and Mezaki 2005: 35, pl. 1, fig. 28; Veron et al. 2016: part, unnumbered figs 4th, 6th in the 1st row, 3rd, 5th in 2nd row.

Paragoniastrea sp.: Sugihara et al. 2015: 153, 4 unnumbered figs; Huang et al. 2014: fig. 6l.

Paragoniastrea sp. HENGE *sensu* Nomura et al. 2016: 11; Nomura 2016: 44, figs A–F, 45 (part), figs A, D, E (B, C, F = *P. australensis*); Nomura et al. 2020: 40, fig. 20, G–I.

Type material. Holotype: MUFS C588 (size 74 × 49 mm), sample MO417, Oshima Island, Nichinan, Miyazaki, Japan (31.527593°N, 131.401469°E), depth 9 m, 14 November 2021, coll. H. Fukami. **Paratypes:** MUFS C78 (size 102 × 88 mm), sample number JP065, Sabiura, Kushimoto, Wakayama, Japan (33.464375°N, 135.785721°E), depth 5 m, 22 October 2012, coll. H. Fukami; MUFS C586 (size 90 × 66 mm), sample AM19-24, Satsuki, Amakusa, Kumamoto, Japan (32.457516°N, 130.207903°E), depth 4 m, 25 July 2019, coll. H. Fukami.

Other material. JAPAN. SMP-HC 894, Takatomi Bay, Kushimoto, Wakayama, depth 10 m, 12 May 2003, coll. K. Nomura; SMP-HC 1038, Tosaki, Kushimoto, depth 6 m, 14 Dec 2003, coll. K. Nomura; SMP-HC 1203, 1205, 1208, Sabiura, Kushimoto, depth 3 m, 23 June 2005, coll. K. Nomura; SMP-HC 1749, Tanami, Kushimoto, depth 3 m, 24 Apr 2009, coll. K. Nomura; SMP-HC 1799, Takatomi Bay, Kushimoto, depth 6 m, 14 July 2009, coll. K. Nomura; SMP-HC 2957, Sabiura, Kushimoto, Wakayama, depth 9 m, 13 Dec 2015, coll. K. Nomura; SMP-HC 3049, Sabiura, Kushimoto, Wakayama, depth 10 m, 4 Feb 2016, coll. K. Nomura; MUFS C585, sample AM19-14, Satsuki, Amakusa, Kumamoto, depth 4 m, 25 July 2019, coll. H. Fukami; MUFS C587, sample NB92, Shimanourashima Island, Miyazaki, depth 13 m, 15 May 2015, coll. H. Fukami; MUFS C589, sample TK89, Takashima Island, Nagasaki, depth 3 m, 24 September 2021, coll. H. Fukami. **TAIWAN.** ASIZC0001666, sample TWN45, Yehliu, New Taipei, depth 11 m, 4 July 2019, coll. H. Fukami (Suppl. material 1).

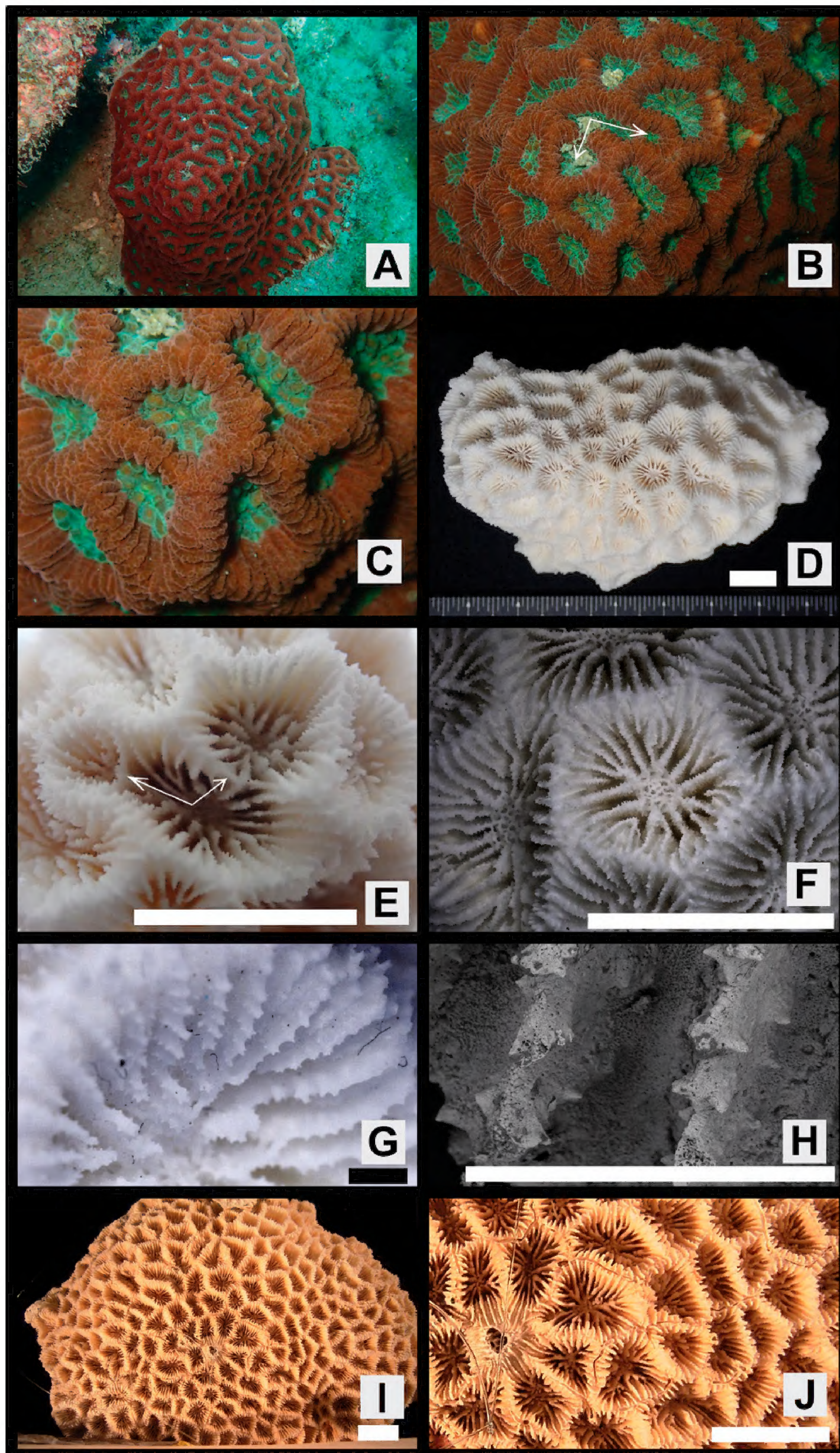


Figure 2. *Paragoniastrea variabilis* sp. nov. (Holotype: MUFS C588) and *Paragoniastrea deformis* (Holotype: MTQ G32487) **A–H** *P. variabilis* **A** colony *in situ* **B** close up of corallite division in two directions **C** close up the colony *in situ* **D** full scale of the skeletal specimen **E** corallite division in two directions from the skeletal specimen **F** corallites of the skeletal specimen **G** close up of one corallite of the skeletal specimen **H** septal teeth of the skeletal specimen **I–J** *P. deformis* **I** full scale of the skeletal specimen, **J** corallites of the skeletal specimen. Scale bar: 10 mm (**D, E, F, I, J**); 1 mm (**G, H**).

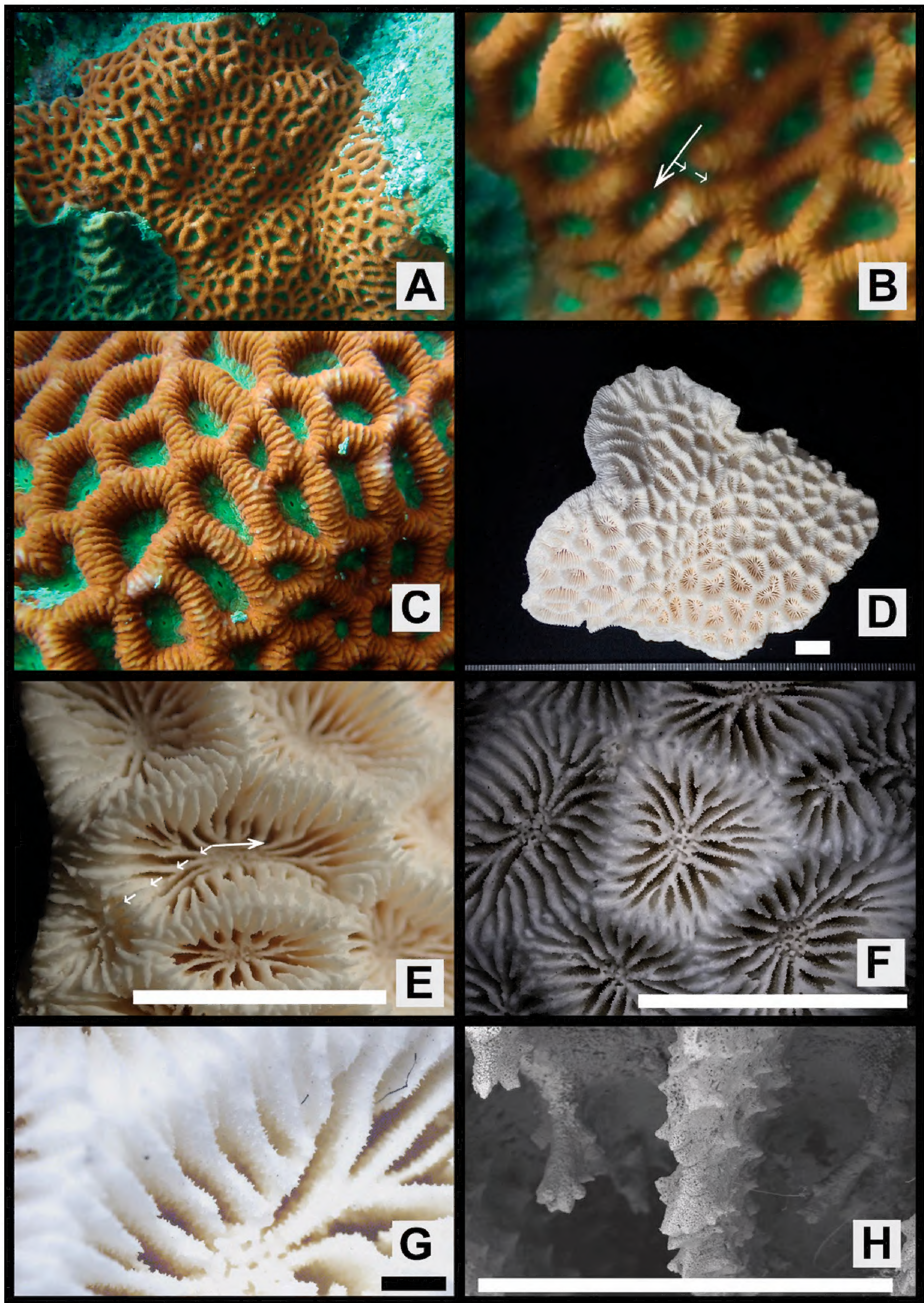


Figure 3. *Paragoniastrea variabilis* sp. nov. (Paratype: MUFS C78). **A** colony *in situ* **B** close up of corallite division in two directions **C** close up the colony *in situ* **D** full scale of the skeletal specimen **E** corallite division in two directions from the skeletal specimen **F** corallites of the skeletal specimen **G** close up of one corallite of the skeletal specimen **H** septal teeth of the skeletal specimen. Scale bar: 10 mm (**D**, **E**, **F**); 1 mm (**G**, **H**).

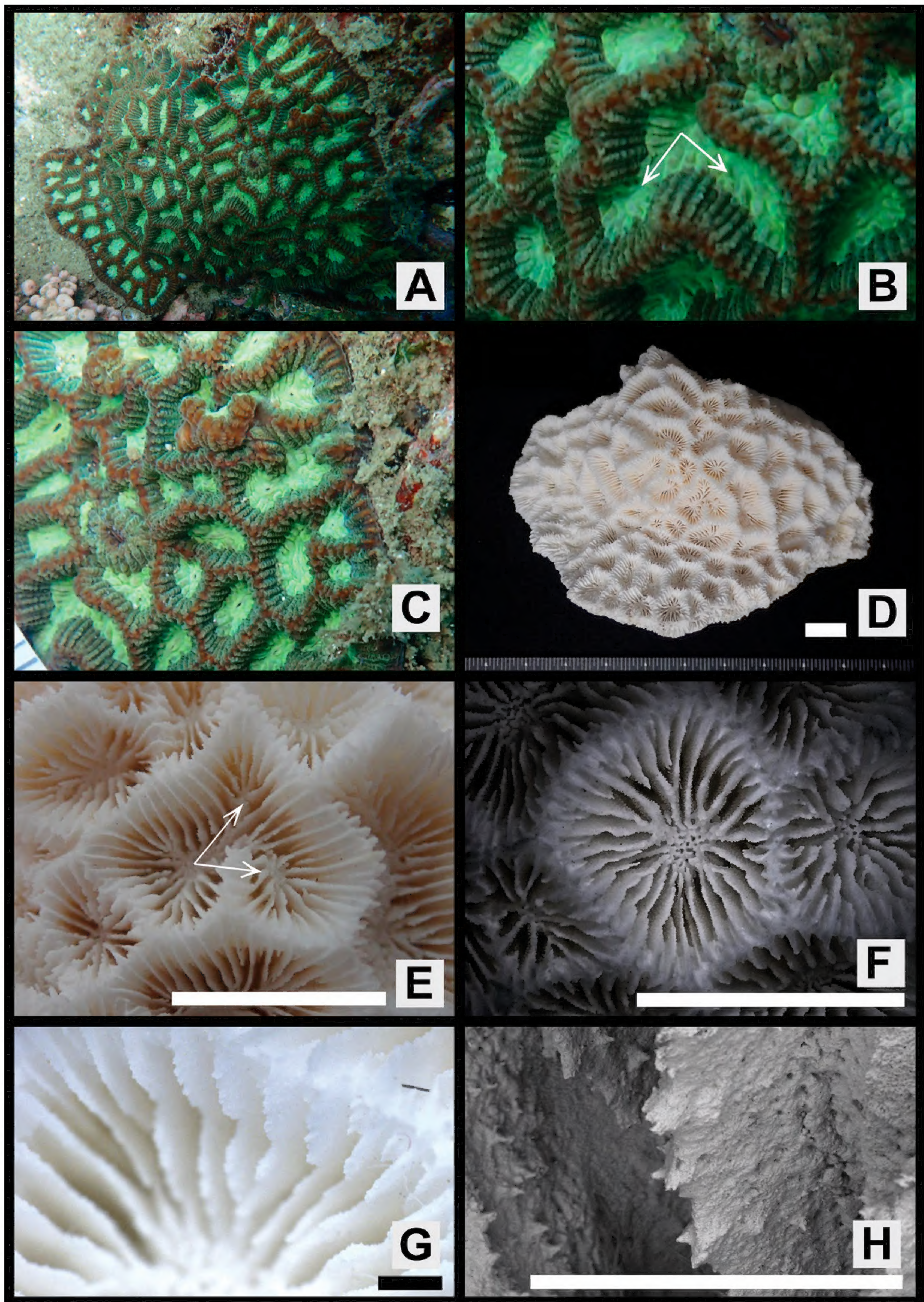


Figure 4. *Paragoniastrea variabilis* sp. nov. (Paratype: MUFS C585) **A** colony *in situ* **B** close up of corallite division in two directions **C** close up the colony *in situ* **D** full scale of the skeletal specimen **E** corallite division in two directions from the skeletal specimen **F** corallites of the skeletal specimen **G** close up of one corallite of the skeletal specimen **H** septal teeth of the skeletal specimen. Scale bar: 10 mm (**D, E, F**); 1 mm (**G, H**).

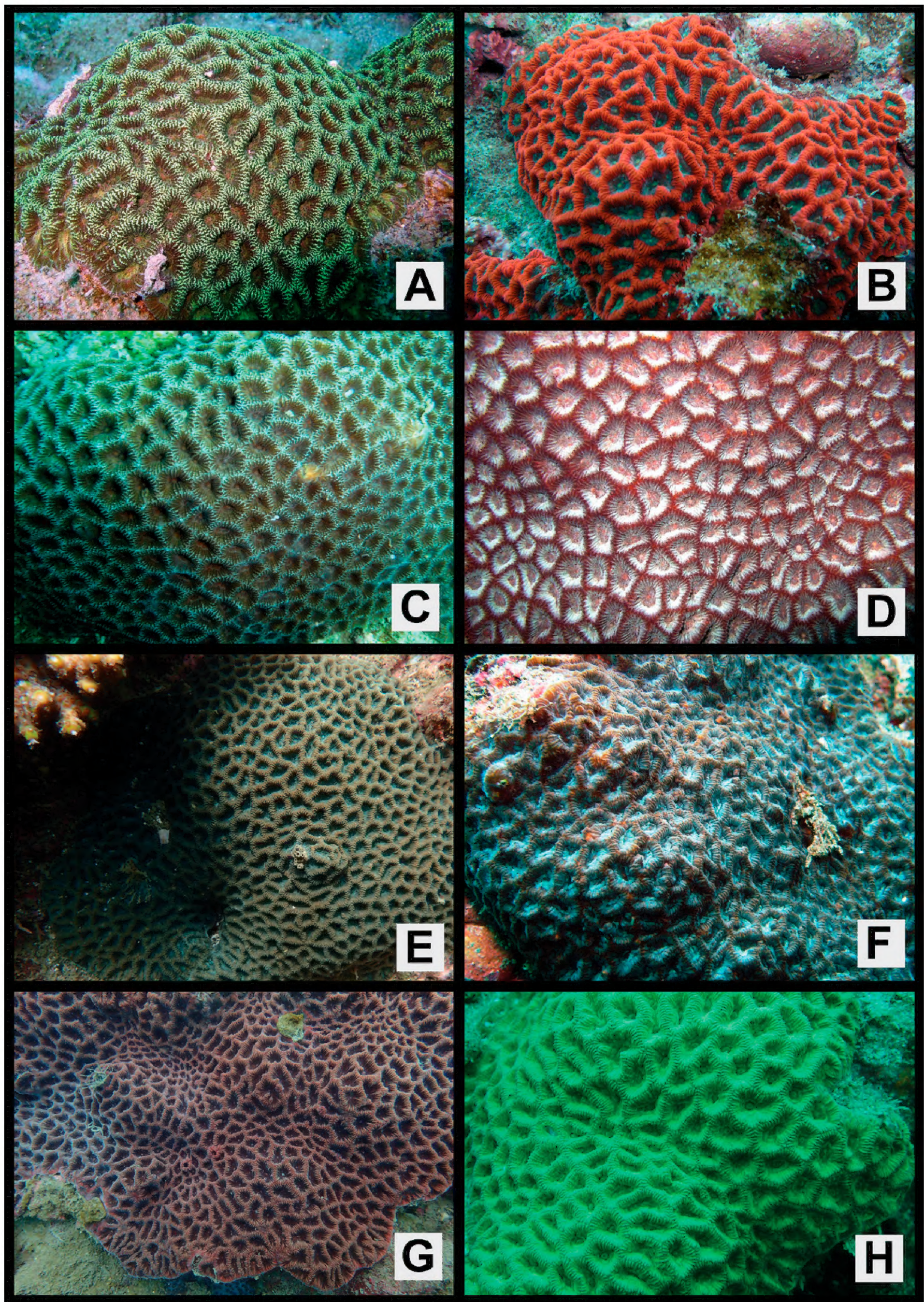


Figure 5. Color variation in life of *Paragoniastrea variabilis* sp. nov. **A** SMP-HC 894, Kushimoto, Wakayama, Japan **B** SMP-HC 1205, Kushimoto, Wakayama, Japan **C** SMP-HC 1749, Amakusa, Kumamoto, Japan **D** SMP-HC 1038, Kushimoto, Wakayama, Japan **E** MUFS C585, Amakusa, Kumamoto, Japan **F** SMP-HC 1208, Kushimoto, Wakayama, Japan **G** ASIZC0001666, Yehliu, New Taipei, Taiwan **H** SMP-HC 1203, Kushimoto, Wakayama, Japan.

Comparative specimens. *Paragoniastrea australensis*. MUFS C571, sample AM19-3, Amakusa, Kumamoto, Japan; MUFS C572, sample AM19-38, Amakusa, Kumamoto, Japan; MUFS C573, sample MO451, Oshima Island, Miyazaki, Japan; MUFS C574, sample MO457, Oshima Island, Miyazaki, Japan; MUFS C575, sample MO461, Oshima Island, Miyazaki, Japan; MUFS C576, sample NB96, Shimanourashima Island, Miyazaki, Japan; MUFS C577, sample NB148, Shimanourashima Island, Miyazaki, Japan; MUFS C578, sample OI10, Fukushima Island, Oita, Japan.

Paragoniastrea deformis. Holotype (MTQ G32487), Kushimoto, Wakayama, Japan; MUFS C579, sample AM19-18, Amakusa, Kumamoto, Japan; MUFS C580, sample AM19-21, Amakusa, Kumamoto, Japan; MUFS C581, sample AM19-26, Amakusa, Kumamoto, Japan; MUFS C582, sample AM19-36, Amakusa, Kumamoto, Japan; MUFS C583, sample MO450, Oshima Island, Miyazaki, Japan; MUFS C584, sample MO452, Oshima Island, Miyazaki, Japan; ASIZC0001667, sample TWN46, Yehliu, New Taipei, Taiwan; ASIZC0001669, sample TWN48, Yehliu, New Taipei, Taiwan.

Paragoniastrea aff. *deformis*. MUFS C590, sample AM19-19, Amakusa, Kumamoto, Japan; SMBL Cni-10321, sample JPO30, Shirahama, Wakayama, Japan; ASIZC0001691, sample TWN79, Yehliu, New Taipei, Taiwan.

Description. Colonies massive or encrusting, surface smooth or rather uneven (Figs 2A, 3A, 4A, 5A–H).

Corallites intratentacular budding, arrangement mainly cerioid, rarely meandroid, 1–3 corallites lined up in one valley between corallite walls, percentage of having two corallites 2–19 (average $\pm$ SD: 8.2 ± 6.0) % and three corallites 0–8 (3.3 ± 3.3) %. Outline distorted quadrangular or pentagonal, usually compressed, calices 6.1–11.8 (average $\pm$ SD: 9.0 ± 1.6) mm in long diameter, moderately deep, height of calice relief (vertical distance from upper margin of corallite walls to columella) 2.0–4.3 (average $\pm$ SD: 3.0 ± 0.7) mm (Figs 2B–F, 3B–F, 4B–F, Table 1).

Septa formed by usually straight plates, steeply sloped along the corallite walls, numerous, present up to 4th cycles, range of number 28–62 (average $\pm$ SD: 44.7 ± 7.8), length uneven, 2.7–5.1 (3.7 ± 0.7) mm length, width of primary septa thin, 0.19–0.26 (0.21 ± 0.02) mm wide, secondary and tertiary septa almost same width as primaries, quaternary septa usually faint. Primary and secondary septa connected to each other, and sometimes tertiary septa connected as well. Primary and secondary, and sometimes part of tertiary septa reaching columella (total number of septa reaching columella 9–21, average $\pm$ SD: 13.5 ± 2.4). Dorsal margin of septa with 4–9 (average $\pm$ SD: 5.6 ± 0.9) teeth. Teeth arranged vertically in single row, and surface covered with multiple spiny-like granules, sometimes with one short ridge on center of lateral faces. Distance between septal teeth is 0.1–0.6 (average $\pm$ SD: 0.31 ± 0.08) mm. Lateral faces of septa with sparsely distributed granules same as septal teeth (Figs 2E–G, 3E–G, 4E–G, Table 1).

Primary and secondary, and partial or all tertiary septa with rather distinct paliform lobes. Paliform lobes 0.68–1.37 (average $\pm$ SD: 1.18 ± 0.15) mm long vertically, uneven in shape and size, with 1–4 (2.1 ± 0.8) teeth on dorsal margin (Figs 2E–G, 3E–G, 4E–G, Table 1).

Columella rather large, spongy, formed by many entangled trabeculae, 0.9–2.8 (average $\pm$ SD: 1.6 ± 0.5) mm in long diameter (Figs 2F, 3F, 4F, Table 1).

Corallite walls joined between adjacent corallites, rather steeply sloped but standing upright even near the center of corallum, rather thin, groove-and-tube structure absent on walls joint (Figs 2D–F, 3D–F, 4D–F).

Table 1. Morphological characteristics of *Paragoniastrea* spp. Left half is average (standard deviation), right half is value range (minimum to maximum). The measurements for each of the characteristics were taken from five corallites per specimen. For characteristics marked with an asterisk, three characters were measured from one corallite and the average of the three characters was treated as data from one corallite. Measurement in mm.

Characteristics	<i>P. variabilis</i> sp. nov.	<i>P. deformis</i>	<i>P. aff. deformis</i>	
	n=16	n=8	n=2 (AM19-19, JP030)	n=1 (TWN79)
Groove-and-tube structure	absent	present	absent	absent
Long diameter of calice	9.0 (1.6), 6.1–11.8	5.4 (0.8), 4.5–7.7	8.6 (1.0), 7.2–10.2	8.2 (0.4), 7.6–8.9
Long diameter of columella	1.6 (0.5), 0.9–2.8	1.5 (0.4), 1.24–2.3	1.9 (0.3), 1.4–2.4	1.8 (0.3), 1.3–2.1
height of calice relief	3.0 (0.7), 2.0–4.3	2.2 (0.6), 1.2–3.6	3.1 (0.7), 2.2–4.6	no data
Width of primary septa*	0.21 (0.02), 0.19–0.26	0.30 (0.02), 0.28–0.34	0.24 (0.02), 0.20–0.30	0.23 (0.02), 0.19–0.26
No. of septa per calice	44.7 (7.8), 28–62	33.1 (3.7), 29–44	66.5 (5.2), 59–76	36.6 (4.1), 32–44
No. of septa reaching collemulla	13.5 (2.4), 9–21	10.8 (1.7), 6–12	21.1 (1.4), 19–24	18.0 (2.1), 16–21
Length of septa*	3.7 (0.7), 2.7–5.1	3.5 (0.8), 1.4–4.1	3.8 (0.7), 2.8–5.1	3.2 (0.7), 2.1–4.4
No. of teeth on septa*	5.6 (0.9), 4–9	5.5 (0.6), 4–8	6.5 (0.5), 5–8	6.9 (0.5), 6–8
Distance between septal teeth*	0.31 (0.08), 0.1–0.6	0.34 (0.09), 0.2–0.6	0.29 (0.06), 0.2–0.4	0.20 (0.03), 0.1–0.3
Hight of paliform lobe*	1.18 (0.15), 0.68–1.37	1.14 (0.17), 0.87–1.37	1.12 (0.13), 0.86–1.27	no data
No. of teeth on paliform lobe*	2.1 (0.8), 1–4	2.3 (0.5), 1–4	3.0 (0.6), 2–4	1.4 (0.3), 1–2
No. of corallites in one valley	up to three, corallites	up to two, corallites	up to two, corallites	up to two, corallites
Percentage of two corallites in a valley	8.2 (6.0), 2–19	4.4 (2.3), 3–8	6.5 (0.8), 6–7	7
Percentage of three corallites in a valley	3.3 (3.3), 0–8	0	0	0

Color in life. Colors are highly variable, usually soft bodies of corallite walls and calices are different. Corallite walls brown, greenish-brown, light greenish-brown, red or reddish-brown; calices brown, light brown, green, greenish-brown or light green (Figs 2A–C, 3A–C, 4A–C, 5A–H).

Distribution and habitat. *Paragoniastrea variabilis* sp. nov. is known from warm-temperate, non-coral reef region in Japan (Wakayama, Kochi, Oita, Nagasaki, Kumamoto, Miyazaki and Kagoshima) and northern Taiwan (Fig. 1), found in shallow water at depths of 3–15 m, and is sympatric with all other species of the *Paragoniastrea* from Japan, namely *P. australensis*, *P. deformis* and *P. aff. deformis*.

Etymology. The species is named from Latin *variabilis* (variable), in reference to the considerable color variations.

Remarks

Differences between species of *Paragoniastrea* based on morphological analysis

Paragoniastrea previously included three species, namely, *P. australensis*, *P. deformis* and *P. russelli* (Huang et al. 2014; Hoeksema and Cairns 2024). This study adds the new species *P. variabilis* sp. nov. (see Key to the species of *Paragoniastrea* below), which is separated from its congeners by following a combination of several characters: (1) The arrangement of corallites is dominantly cerioid, rarely meandroid; (2) Primary septa are not clearly thicker than secondary septa; and (3) the groove-and-tube structure is absent on corallite wall joint.

The new species most closely resembles *P. deformis* in *Paragoniastrea* (Figs 2, 7). Both species have significant differences not only in the presence or absence of

groove-and-tube structure but also in the following characteristics. *Paragoniastrea variabilis* sp. nov. has a larger average calice diameter ($p < 0.001$), average number of septa per calice ($p < 0.001$), and average number of septa reaching columella ($p < 0.001$) than *P. deformis*. In addition, *P. deformis* has wider primary septa than *P. variabilis* sp. nov. ($p < 0.001$) and up to two corallites in one valley between corallite walls, whereas *P. variabilis* sp. nov. has up to three corallites (Figs 2, 6, 7, Table 1).

Identifying the species, two specimens of sample AM19-19 (MUFS C590) from Kumamoto and JP030 (SMBL Cni-10321) from Wakayama, which were identified as *P. deformis* by Huang et al. (2014), had more septa per calice and more septa reaching columella than *P. deformis* and *P. variabilis* sp. nov. Although these specimens are morphologically different from known species, sufficient molecular phylogenetic evidence has not been obtained. Therefore, these specimens were tentatively treated as *Paragoniastrea* aff. *deformis*. In addition, one specimen, TWN79 (ASIZC0001691) from Taiwan, has similar morphological characteristics to *P. variabilis* sp. nov., but phylogenetic analysis showed this sample was included in the *P. deformis* clade in the IGR tree but formed an independent clade with specimen JP030 identified as *P. aff. deformis*, apart from *P. deformis* and *P. variabilis* sp. nov. in the ITS tree (see below molecular phylogenetic analysis). Thus, this specimen was treated as *P. aff. deformis*.

Principal component analysis using long diameter of columella, width of primary septa, number of teeth on septa, long diameter of columella, number of septa per calice, and number of septa reaching columella divided our samples into three groups. Among them, *P. variabilis* sp. nov. and *P. deformis* were separated along the PC1 axis, with PC1 explaining 47.9% of the morphological multivariate variance. *Paragoniastrea* aff. *deformis* was also distinct from *P. deformis* along the PC1 axis, but it partially overlapped with *P. variabilis* sp. nov. (Fig. 8).

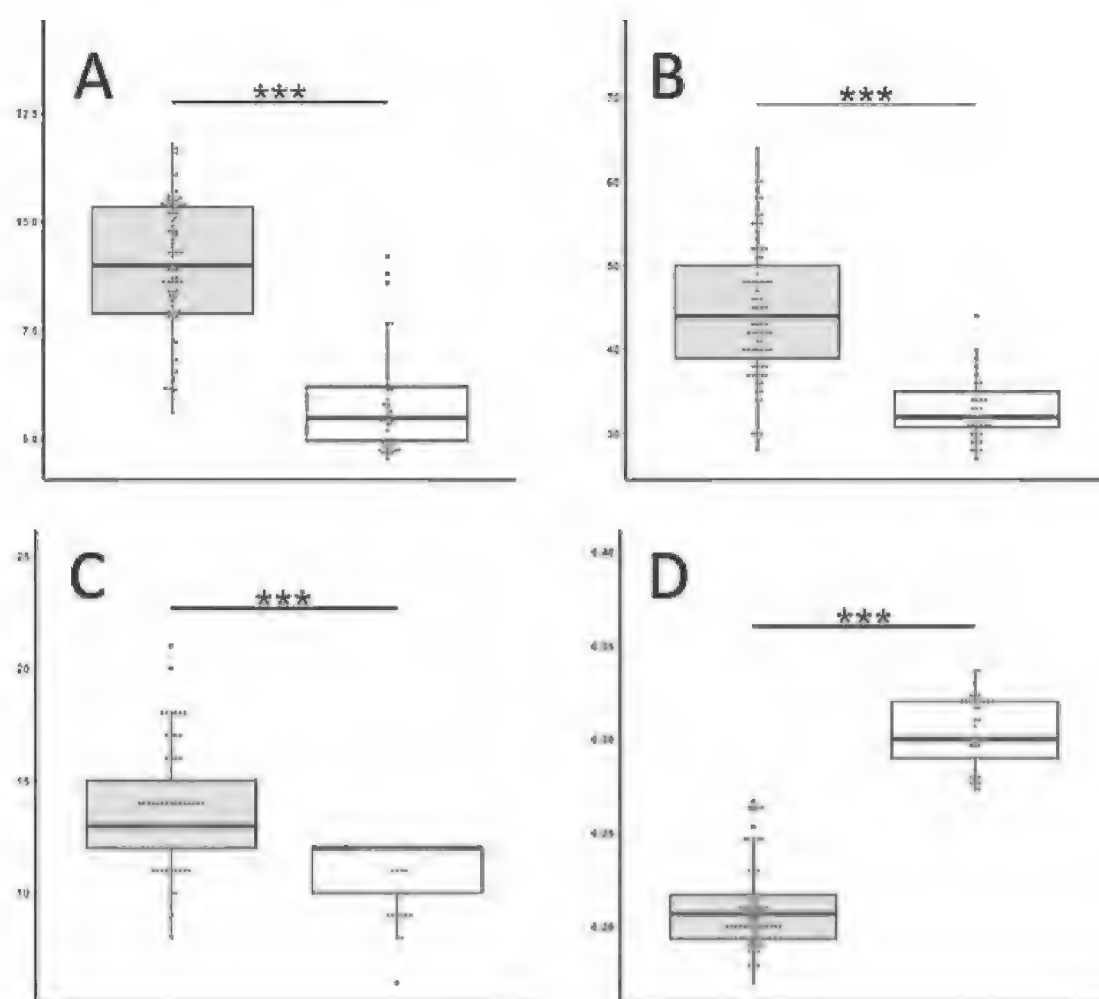


Figure 6. Morphological comparison between *P. variabilis* sp. nov. (left) and *P. deformis* (right) **A** long diameter of calice **B** number of septa per calice **C** number of septa reaching to columella **D** width of primary septa. Vertical bars indicate standard deviations, and the black horizontal line in the box-and-whisker chart indicates the median. ***: $p < 0.001$.

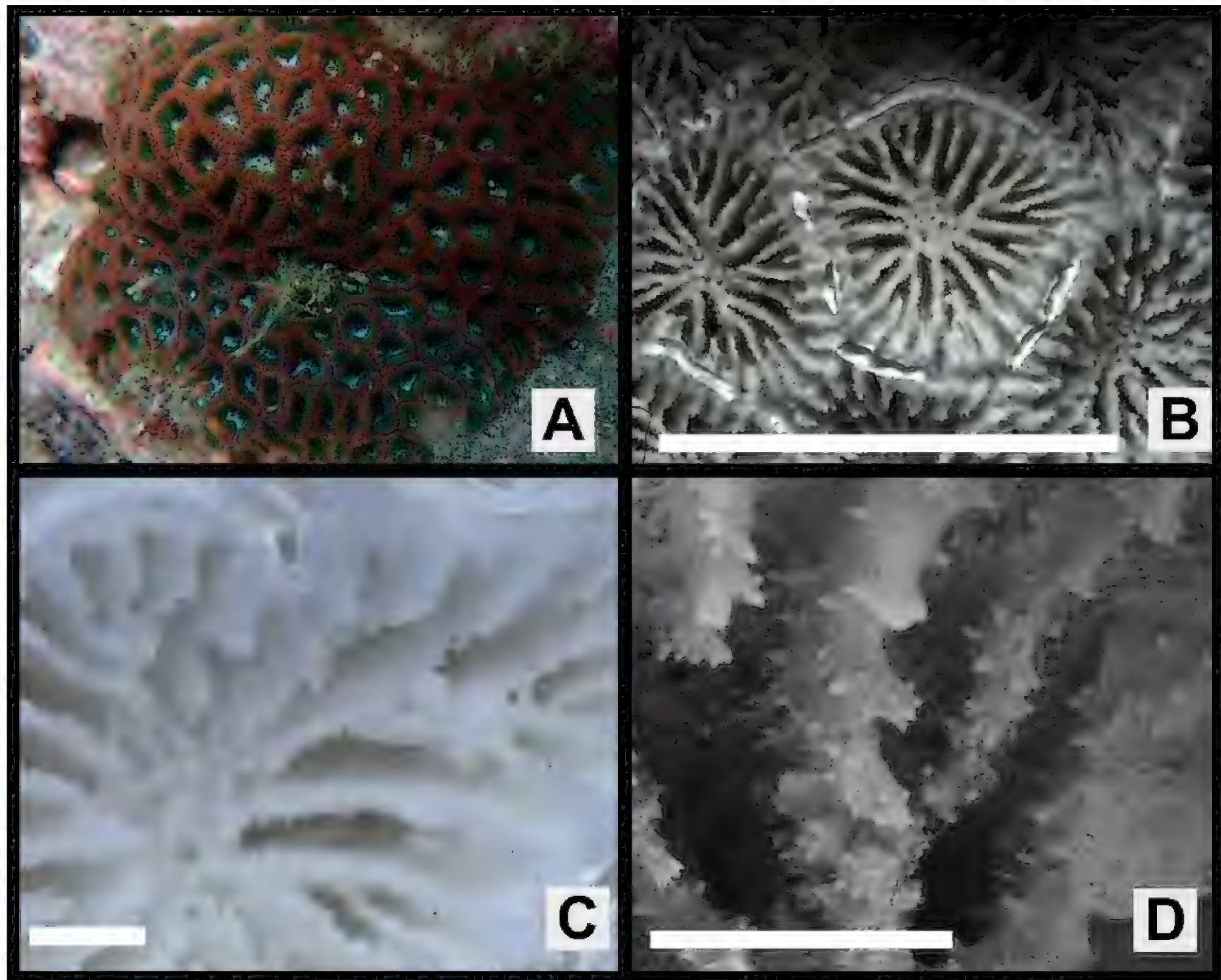


Figure 7. *Paragoniastrea deformis* (MUFS C580) **A** colony *in situ* **B** corallites of the skeletal specimen **C** close up of one corallite of the skeletal specimen **D** septa and septal teeth. Scale bars: 10 mm (**B**); 1 mm (**C**, **D**).

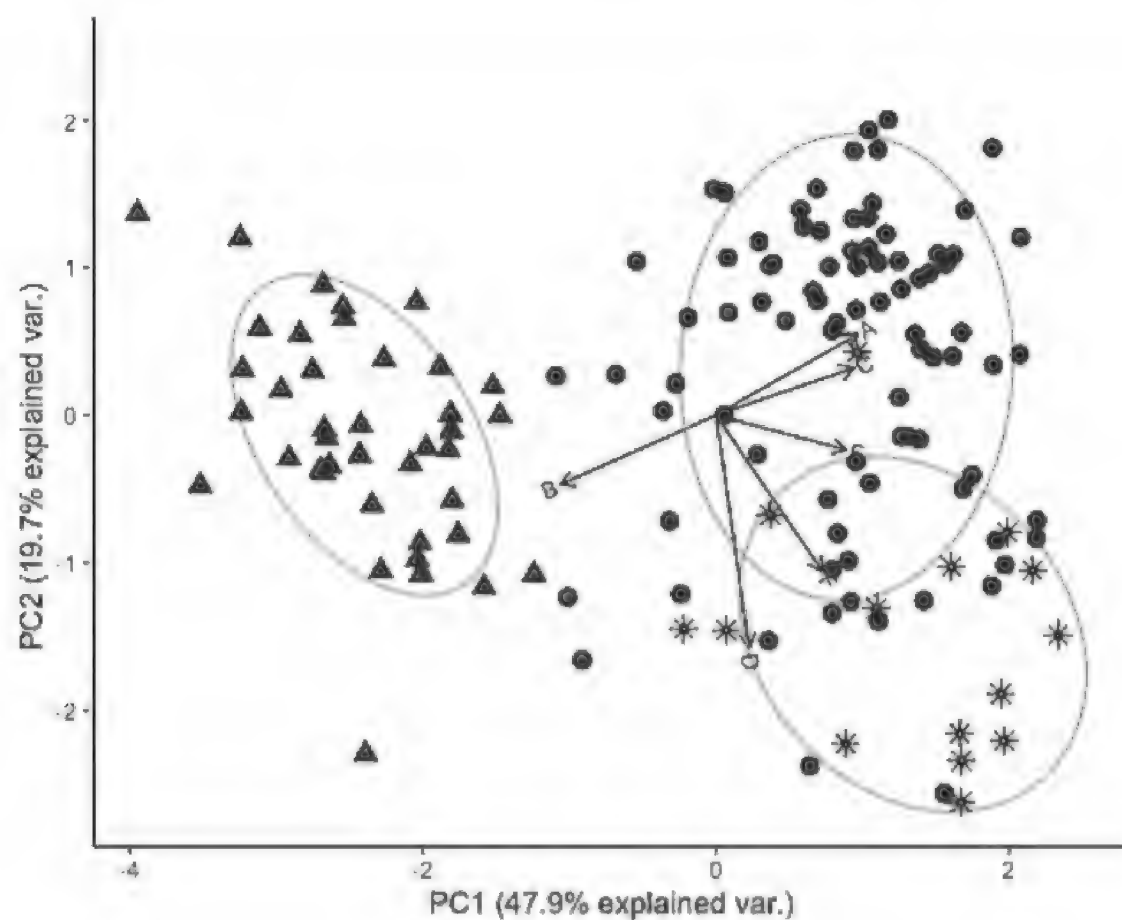


Figure 8. Principal component analysis on morphological characteristics of specimens in *P. variabilis* sp. nov. (black circle), *P. deformis* (black triangle) and *P. aff. deformis* (black asterisk). Arrows indicate long diameter of calice (**A**), width of primary septa (**B**), number of teeth on septa (**C**), long diameter of columella (**D**), number of septa per calice (**E**), number of septa reaching columella (**F**).

Key to the species of *Paragoniastrea*

- 1 Corallites arrangement procoid, cerioid or meandroid, width of primary septa clearly thicker than secondary septa.....***P. russelli***
- Corallites arrangement cerioid or meandroid, width of primary septa not clearly thicker than secondary septa**2**
- 2 Corallites arrangement of meandroid dominant***P. australensis***
- Corallites arrangement cerioid dominant, meandroid rare.....**3**
- 3 Groove-and-tube structure present on joint of corallite walls.....***P. deformis***
- Groove-and-tube structure absent on joint of corallite walls.....
.....***P. variabilis* sp. nov.**

Differences between species of *Paragoniastrea* based on molecular phylogenetic analysis

For the IGR marker, the overall sequence length was 894 nucleotides with 102 polymorphic sites. The molecular phylogenetic tree of IGR showed that *P. variabilis* sp. nov. formed an independent clade from the other clades, including *P. deformis*, *P. australensis* and *P. russelli*. All three samples, AM19-19 (MUFS C590), TWN79 (ASTZC0001691), and JP030 (SMBL Cni-10321) of *P. aff. deformis* were included within the clade of *P. deformis* (Fig. 9).

For the ITS marker, the overall sequence length was 774 nucleotides with 69 polymorphic sites. The ITS tree showed that *P. deformis* and *P. variabilis* sp. nov. were also clearly separated into different clades (Fig. 9). Two samples (TWN79

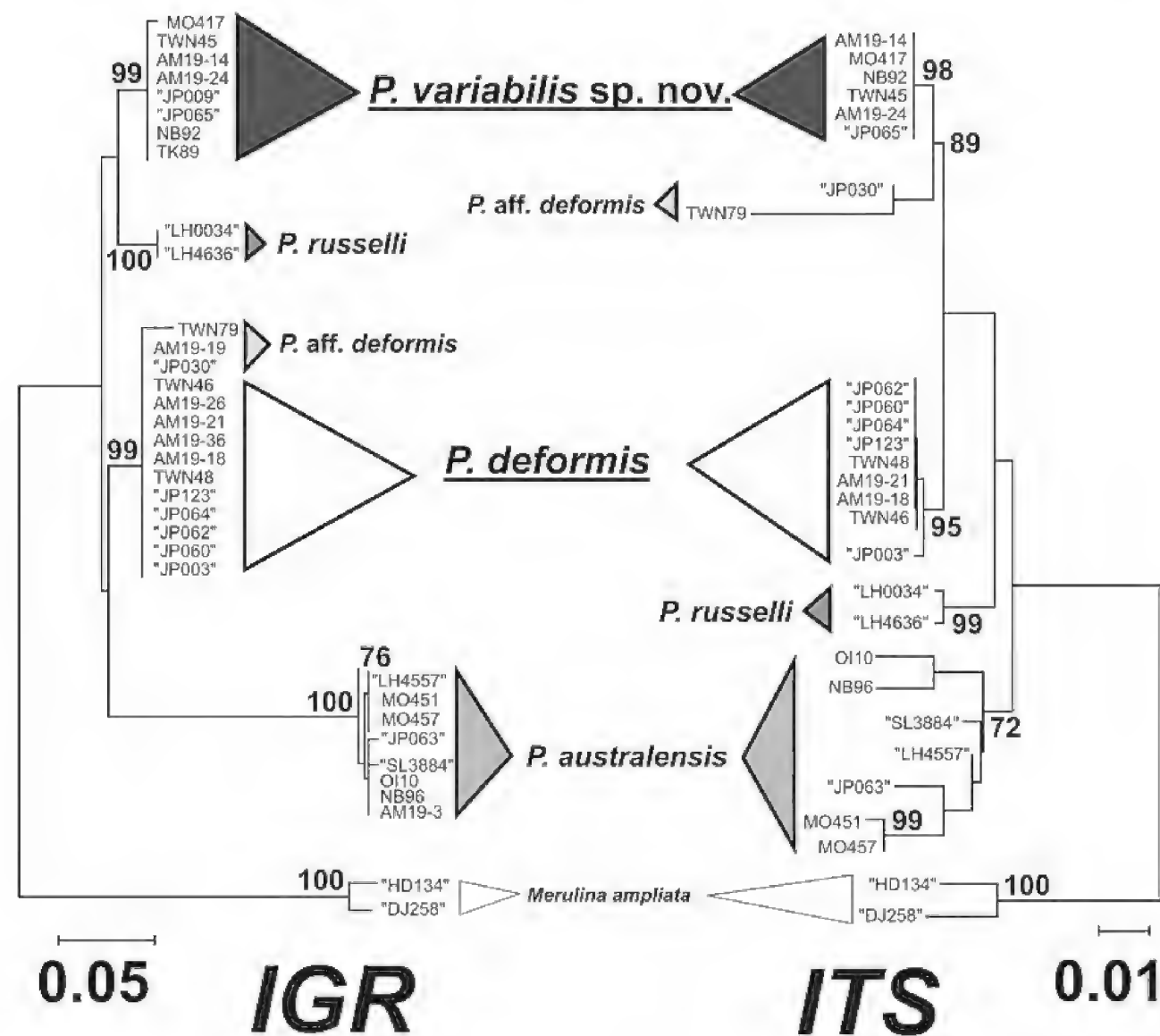


Figure 9. Molecular phylogenetic tree based on IGR (left) and ITS (right) for *Paragoniastrea* species. DNA sequences obtained from DDBJ were shown with double quotation marks with the specimen number.

and JP030) of *P. aff. deformis* formed an independent clade. The third sample (AM19-19) of *P. aff. deformis* could not be used for this analysis because of PCR amplification failure.

Conclusion

Paragoniastrea variabilis sp. nov. had been considered an intraspecific morphological variant of *P. deformis* because of their sympatric distributions and similar morphology (see synonymy). In this study, the results of morphological and molecular phylogenetic analyses showed that *P. variabilis* sp. nov. and *P. deformis* are clearly distinct from each other. Thus, we describe *P. variabilis* sp. nov. as a new species of *Paragoniastrea*.

Finally, the taxonomic position of *P. aff. deformis* (Fig. 10) remains unclear because of insufficient morphological and phylogenetic studies, so better sampling and analyses will be needed to clarify its species status.

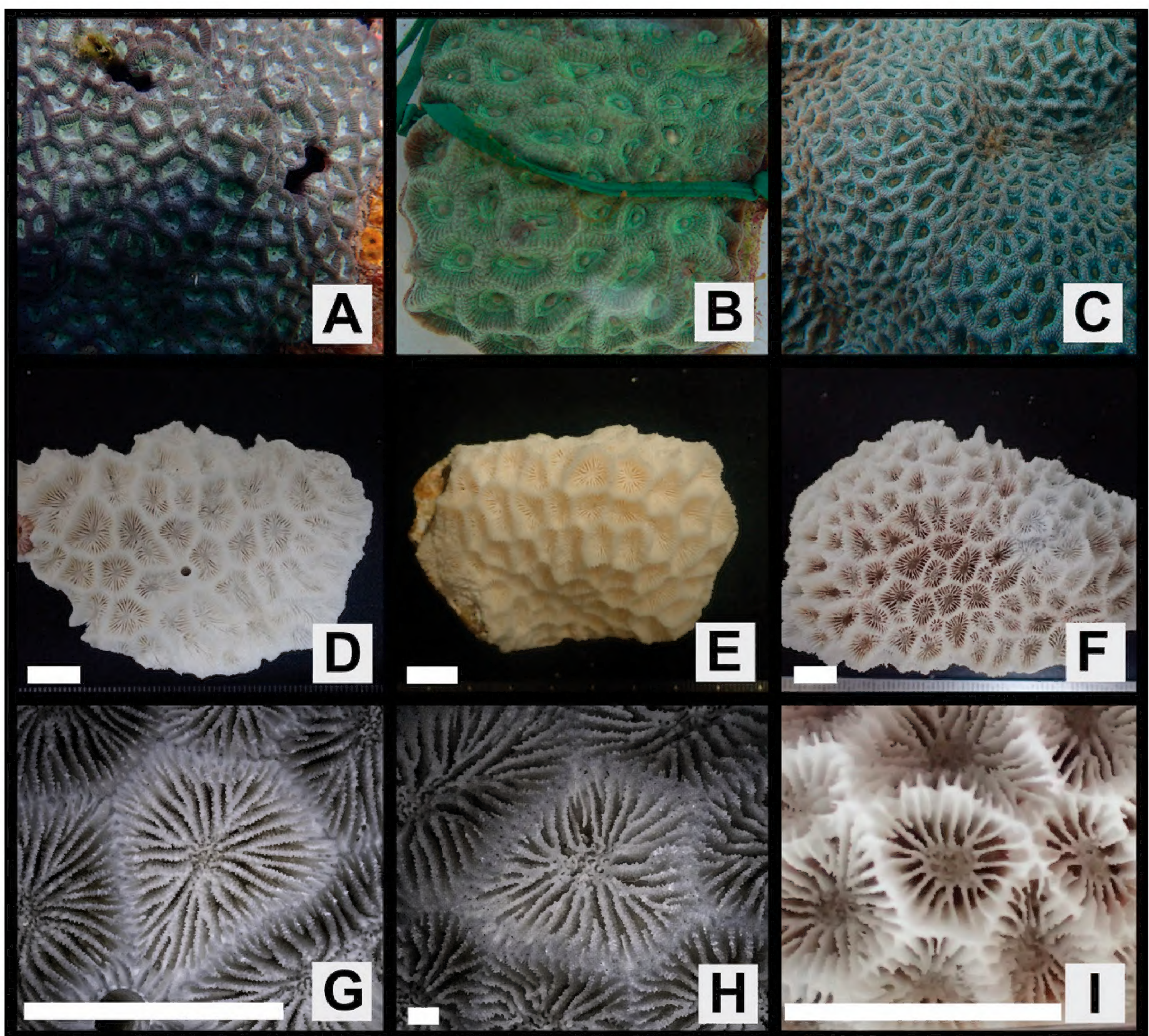


Figure 10. *Paragoniastrea. aff. deformis* **A–C** colonies *in situ* **D–F** full scale of the skeletal specimens **G–I** corallites of the skeletal specimens **A, D, G** MUFS C590 (AM19-19), Amakusa, Kumamoto Japan **B, E, H** ASIZC0001691 (TWN79), Yehliu, New Taipei, Taiwan **C, F, I** SMBL Cni-10321 (JP030), Kushimoto, Wakayama, Japan. Scale bar: 10 mm (**D–G, I**); 1 mm (**H**).

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Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

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Author contributions

Data curation: DK, HF, SA, YN, KN. Formal analysis: DK. Investigation: HF. Project administration: HF. Writing - original draft: KN, DK, HF. Writing - review and editing: YN, SA.

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Data availability

All of the data that support the findings of this study are available in the main text or Supplementary Information.

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Supplementary material 1

List of specimens that we collected or used in this study

Authors: Daigo Kishi, Keiichi Nomura, Yoko Nozawa, Seiji Arakaki, Hironobu Fukami

Data type: xlsx

Explanation note: Sample information including sampling sites and DNA sequences.

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Link: <https://doi.org/10.3897/zookeys.1205.121507.suppl1>

Supplementary material 2

List of species of *Paragoniastrea* referred from Huang et al. (2014) and used in molecular phylogenetic analysis

Authors: Daigo Kishi, Keiichi Nomura, Yoko Nozawa, Seiji Arakaki, Hironobu Fukami

Data type: xlsx

Explanation note: Sample list of referred DNA sequences.

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